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COMPOSITA SUBTILITA (BRACHIOPODA) IN THE WREFORD MEGACYCLOTHEM (LOWER PERMIAN) IN NEBRASKA, KANSAS, AND OKLAHOMA[1]

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ABSTRACT

Brachiopods are abundant and widely distributed in the Lower Permian Wreford Megacyclothem in Nebraska, Kansas, and Oklahoma. Taxa recognized include *Lingula, Orbiculoidea, Petrocrania, Enteletes, Derbyia,* chonetids, productids, *Wellerella, Cleiothyridina,* and *Composita.*

Abundant, well-preserved, and widely distributed Wreford specimens of the spiriferid *Composita* were studied in detail. Because the Wreford *Composita* population consists of an intergradational series of individuals that cannot be separated into clearly distinct groups interpretable as separate species, these fossils are best included in a single species, *Composita subtilita* (Hall, 1852). Two distinct morphotypes were recognized as end members of this intergrading population. These two end members do not differ significantly in distribution and abundance, occurrence in rock types, stratigraphic horizons, or geographic regions; thus, they cannot be explained as ecotypes, evolutionary populations, or subspecies, but can be regarded most appropriately as intraspecific morphotypes. Moreover, although Wreford *Composita* specimens are highly variable in morphology, no systematic variations are apparent which could be attributed to ecologic, evolutionary, or clinal difference. Finally, salinity or sediment influx may have been important limiting environmental factors for the Wreford *Composita subtilita;* extensive shell beds involving this species covered the southern reaches of the sea floor at certain times during Wreford deposition.

INTRODUCTION

The stratigraphy and environments of deposition of the Lower Permian Wreford Megacyclothem have been thoroughly described (Hattin, 1957; Cuffey, 1967; Newton, 1971; Garihan, 1973; Lutz-Garihan and Cuffey, in press), thus providing excellent background for paleontologic studies (Cuffey, 1967; Newton, 1971; Warner and Cuffey, 1973; this paper). The Wreford crops out in a north-south belt extending from southernmost Nebraska, through Kansas, into northern Oklahoma (Newton, 1971, p. 11). The Wreford Megacyclothem includes these stratigraphic units: the Speiser Shale; the Threemile Limestone Member, Havensville Shale Member, and Schroyer Lime-

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stone Member of the Wreford Limestone; and the Wymore Shale Member of the Matfield Shale.

Because the Wreford biota includes abundant and diversified brachiopods that previously had not been studied via the detailed approaches profitably applied to the bryozoans contained in the Wreford, the brachiopods have much potential for paleobiologic investigations. Consequently, over 10,000 brachiopods have been collected throughout the Wreford outcrop belt, each specimen precisely located in terms of its geographic locality, stratigraphic horizon, and lithologic occurrence. Such large population-sized samples make possible thorough study of the morphology and variability exhibited by these brachiopods, and thus they enable the paleontologist to recognize among them species that more closely approach paleobiologic species concepts than has often been the case in paleontologic practice. Also, conclusions may be made concerning possible interrelationships among variabilities induced by taxonomic, evolutionary, stratigraphic, geographic, and paleoecologic causes.

This paper treats in detail one of the Wreford brachiopod genera, *Composita* (see also Garihan, 1973), because its members are abundant within the Wreford Megacyclothem, well preserved, taxonomically challenging, and highly variable in their stratigraphic, lithologic, and geographic occurrence. Communications from brachiopod specialists suggested that *Composita* constituted an extremely difficult group to treat taxonomically at the species level. However, the Wreford forms comprise a very large sample, and such samples when studied by the methods contemplated for this investigation have significantly advanced paleobiologic understanding in the case of various Wreford bryozoan groups. Moreover, even though these animals are morphologically rather simple externally, significantly more extensive numerical characterization of their features could be accomplished than had been previously, in order 1) to help resolve taxonomic problems and 2) to indicate to what causes—stratigraphic or evolutionary, lithologic or paleoecologic, geographic or clinal—observable morphologic variability might be attributed. Finally, the use of numerical as well as qualitative methods helps in the formulation of a thorough description of an Early Permian population of *Composita subtilita,* which can serve as a point of comparison for investigators concerned with the evolution of late Paleozoic *Composita* species.

ACKNOWLEDGMENTS

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METHODS OF INVESTIGATION OF THE WREFORD BRACHIOPODS

COLLECTING LOCALITIES

Most of the brachiopods used in this study were collected from localities already adequately described by Cuffey (1967, p. 18-20, 89-94) and Newton (1971, p. 15-16); others were obtained from new localities included in the following list (Fig. 1). To maintain consistency, I have continued the format and nomenclature of Cuffey and Newton. After the number and description of each locality, the stratigraphic units exposed there are indicated in terms of the informal divisions (lower *(l),* middle *(m),* and upper *(u)*) of the units containing the Wreford Megacyclothem —the Speiser Shale (Sp); the Threemile Limestone Member (Wt), Havensville Shale Member (Wh), and Schroyer Limestone Member (Ws) of the Wreford Limestone; and the Wymore Shale Member (Mw) of the Matfield Shale. Following this, the condition of exposures at the locality is indicated, whether very good (VG), good (G), fair (F), poor (P), or very poor (VP). Published references to the particular locality are cited where appropriate.

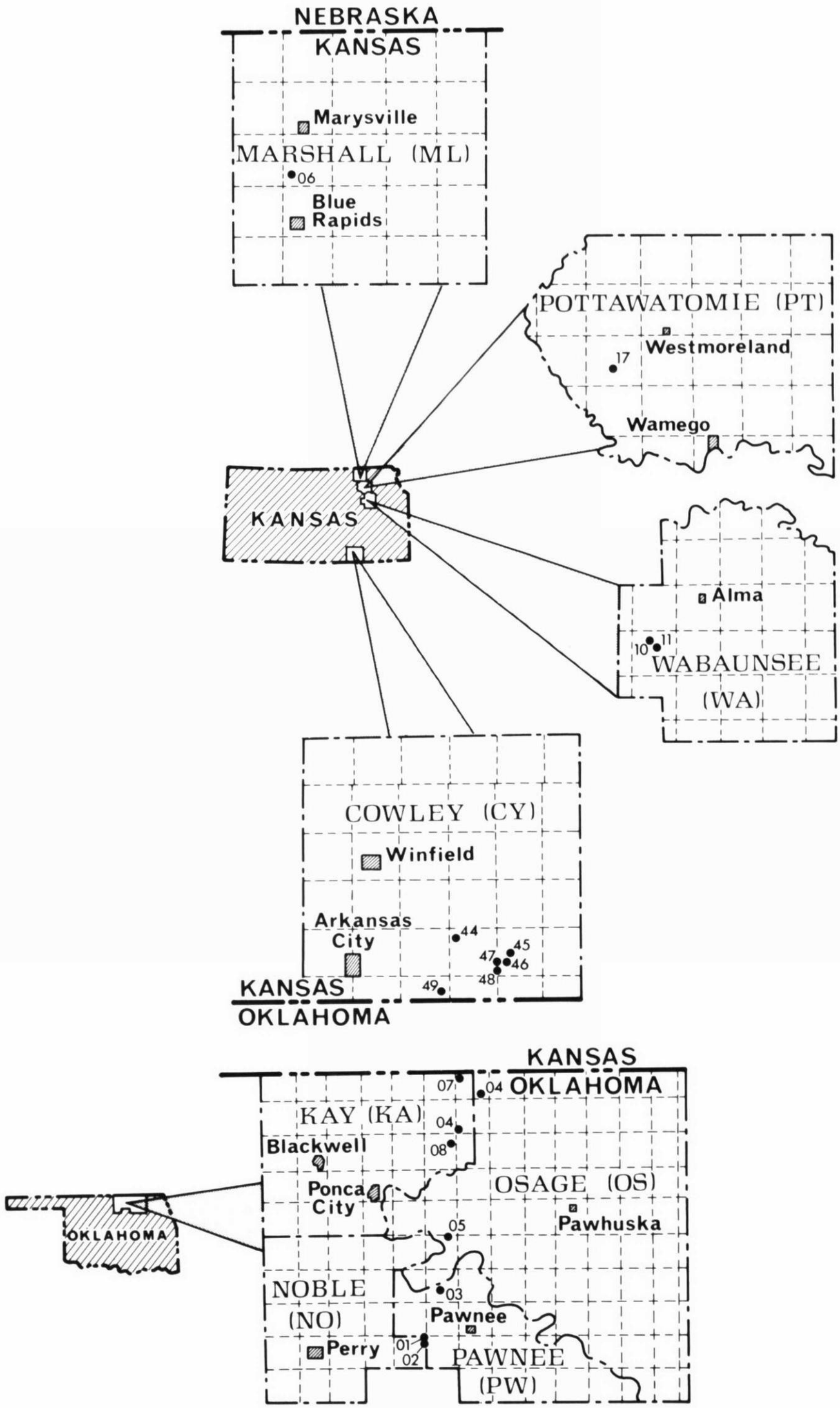

FIG. 1. Wreford localities in Kansas and northern Oklahoma described in text.

Cowley County, Kansas

CY44: Field gully and road ditch on north side of U.S. Hwy. 166, 0.3 mile north of spillway for Cowley County State Lake; SE¼ NE¼ SE¼ sec. 7, T. 34 S., R. 6 E. *u*Ws-*u*Mw; P.

CY45: Gully just south of county road, 1.1 miles east of Otto; NW¼ NW¼ sec. 29, T. 34 S., R. 7 E. *m*Sp-*u*Wt; G.

CY46: Road cut on county road, 1.6 miles southeast of Otto; SW¼ SE¼ SE¼ sec. 30, T. 34 S., R. 7 E. *m*Sp-*u*Wt; F

CY47: Road cut on county road, 1.1 miles south of Otto; NW corner sec. 31, T. 34 S., R. 7 E. *l*-*u*Wt; F.

CY48: Road ditch on county road, 1.5 miles south of Otto; NW¼ NW¼ SW¼ sec. 31, T. 34 S., R. 7 E. *m*Sp-*u*Wt; F.

CY49: Stream cut just north of county road, 4.2 miles southwest of Otto; NW corner sec. 13, T. 35 S., R. 6 E. *l*-*u*Wt; F.

Kay County, Oklahoma

KA04: Road cuts on county road, 0.0-0.2 mile east of junction of county roads; SW¼ SW¼ sec 31, T. 28 N., R. 5 E. *m*Sp-*m*Mw; F.

KA07: Stream cut, just south of county road, 0.8 mile northwest of Hardy; NE¼ NW¼ NW¼ sec. 19, T. 29 N., R. 5 E. *u*Wt-*m*Ws; G.

KA08: Hillside, 0.7 mile southwest of junction of county roads; SE¼ NE¼ NW¼ sec. 12, T. 27 N., R. 4 E. *l*Sp-*u*Wt; F.

Marshall County, Kansas

ML06: Hillside just east of county road, 1.0 mile south of Schroyer; SE corner sec. 30, T. 3 S., R. 7 E. *l*Ws-*u*Mw; P; Hattin, 1957, p. 145 (loc. 10).

Noble County, Oklahoma

N001: Road ditch along county road, 0.9 mile north of Lela; NE¼ NE¼ NE¼ sec. 1, T. 21 N., R. 3 E. *m*Sp and *m*Mw; P.

N002: Road ditch along county road, 0.8 mile north of Lela; SE¼ NE¼ NE¼ sec. 1, T. 21 N., R. 3 E. *m*Sp and *m*Mw; P.

Osage County, Oklahoma

OS04: Road cut on county road, 4.1 miles west of Grainola; SW corner sec. 35, T. 29 N., R. 5 E. *l*-*u*Wt; G.

OS05: Road ditch along county road, 0.7 mile east of junction of county roads; NE¼ NW¼ NE¼ sec. 2, T. 24 N., R. 4 E. *m*Sp, *u*Wt, and *m*Mw.

Pawnee County, Oklahoma

PW03: Road cut on county road, 0.1 mile west of bridge over Walker Creek; SE corner SW¼ sec. 21, T. 23 N., R. 4 E. *l*-*m*Sp; F; Greig, 1959, p. 101-105.

Pottawatomie County, Kansas

PT17: Road cut on Kan. Hwy. 13, 0.1 mile north of junction with county road; NW¼ NW¼ SW¼ sec. 22, T. 8 S., R. 8 E. *l*-*u*Mw; VG.

Wabaunsee County, Kansas

WA10: Road cut on county road, 1 mile southeast of Volland; NE¼ SW¼ sec. 10, T. 13 S., R. 9 E. *l*Sp-*l*Ws; VP; Hattin, 1957, p. 146 (loc. 42).

WA11: Stream bed, 1.5 miles southeast of Volland; NE¼ NE¼ sec. 15, T. 13 S., R. 9 E. *m*Ws; VP; Hattin, 1957, p. 146 (loc. 43).

MEASUREMENTS OF COMPOSITA SUBTILITA

After applying standard collecting and processing procedures, several measurements were made on each uncrushed specimen of *Composita.* Previous workers have included in their descriptions only overall length, width, and thickness (or depth) as measures of shell morphology, supplementing other qualitative observations. Additional information shown by *Composita* shells can also be quantified; such measurements when summarized statistically aid greatly in showing that there is intergradation among the morphological variants within the *Composita* population-sized sample.

The following section defines the quantities measured (Fig. 2). Not all quantities were measurable on every specimen, owing to varying degrees of breakage or distortion.

ALMA—Angle (in degrees) formed by anterolateral margins of shell, measured with contact

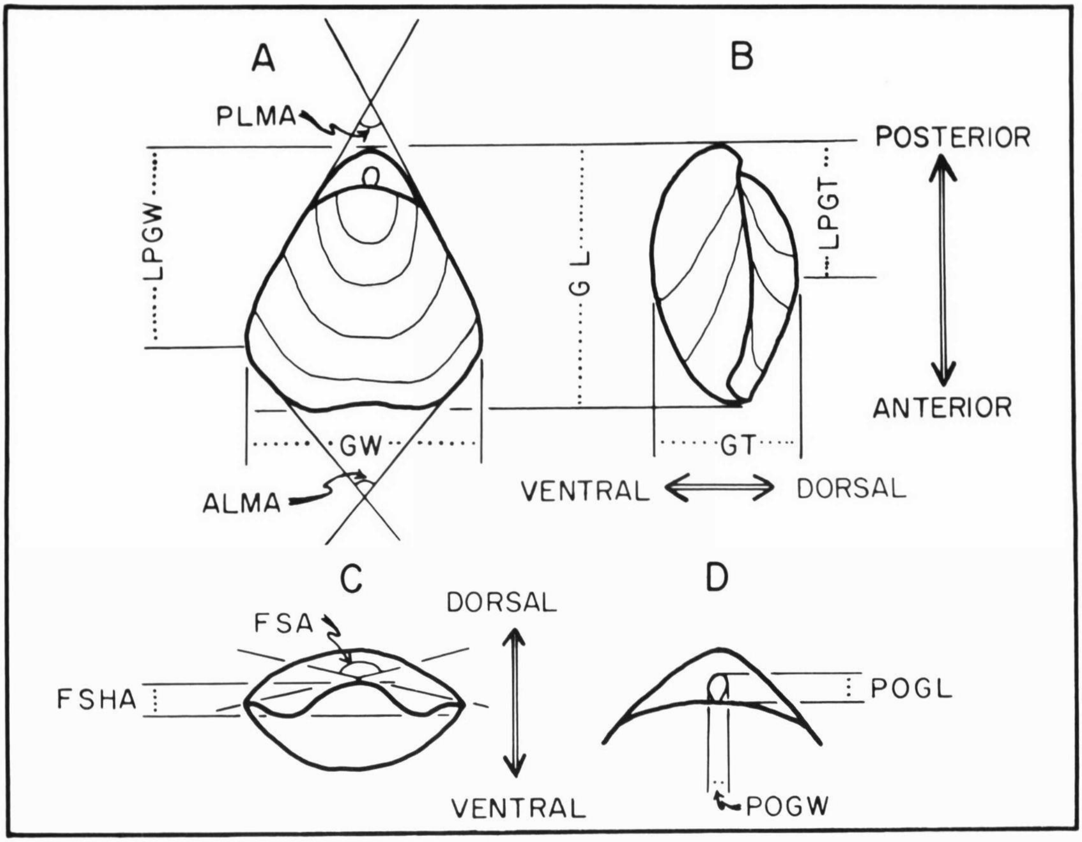

FIG. 2. Four views of *Composita subtilita,* showing morphological characters measured on Wreford specimens.——*A,* dorsal view; *B,* lateral view; *C,* anterior view; *D,* enlargement of dorsal view showing pedicle opening. [Explanation: *ALMA,* angle formed by anterolateral margins of shell; *FSA,* fold and sulcus angle; *FSHA,* height of fold and sulcus; *GL,* greatest length; *GT,* greatest thickness; *GW,* greatest width; *LPGT,* length position of greatest thickness; *LPGW,* length of position of greatest width; *PLMA,* angle formed by posterolateral margins; *POGL,* greatest length of pedicle opening; *POGW,* greatest width of pedicle opening. See text for fuller explanation.]

goniometer; not measured on shells lacking fold and sulcus, because no clearly distinct anterolateral margins are then visible.

FSA—Fold and sulcus angle (in degrees), measured with contact goniometer in plane parallel to plane formed by greatest width and greatest thickness of shell; points determining this angle are shown in Figure 2.

FSHA—Height (in millimeters) of fold and sulcus, measured by caliper parallel to plane of bilateral symmetry and parallel to maximum thickness of shell. This morphologic character was important to earlier brachiopod students in differentiating species and varieties of *Composita,* but previously was determined only qualitatively; that is, a fold and sulcus was described as smaller or larger than another but not precisely measured.

GL—Greatest length (in millimeters) of brachiopod shell, measured by caliper as maximum length parallel to plane of bilateral symmetry (Grinnell and Andrews, 1964, p. 238).

GT—Greatest thickness (in millimeters) of brachiopod shell (also known as depth), measured by caliper as maximum thickness perpendicular to line from dorsal beak to anterior commissure and parallel to plane of bilateral symmetry (Grinnell and Andrews, 1964, p. 239).

GW—Greatest width (in millimeters) of brachiopod shell, measured by caliper as maximum width parallel to plane of commissure and perpendicular to plane of bilateral symmetry (Grinnell and Andrews, 1964, p. 238-239).

LPGT—Length position (in millimeters) of greatest thickness, measured by caliper along length of shell as distance from posterior margin to position of maximum thickness; this parameter has not previously been measured, but rather referred to only qualitatively, as in the phrase "greatest thickness posterior to mid-length" (Sturgeon and Hoare, 1968, p. 57).

LPGW—Length position (in millimeters) of greatest width, measured by caliper along length of brachiopod as distance from posterior margin to position of maximum width; *LPGW* has been referred to only qualitatively in previous work.

PLMA—Angle (in degrees) formed by posterolateral margins of shell, measured by contact goniometer; this is another quantity previously described only qualitatively, that is, as either an acute or an obtuse angle (Sturgeon and Hoare, 1968, p. 57-59).

POGL—Greatest length (in millimeters) of pedicle opening, measured by caliper as maximum length parallel to plane of bilateral symmetry.

POGW—Greatest width (in millimeters) of pedicle opening, measured by caliper as maximum width perpendicular to plane of bilateral symmetry and perpendicular to POGL.

DISTRIBUTION OF THE BRACHIOPOD ASSOCIATES OF WREFORD COMPOSITA SUBTILITA

Several different groups of brachiopods occur in rocks of the Wreford Megacyclothem. Only *Composita* has thus far been studied in detail; however, I am currently studying the other brachiopod groups. These include productids (possibly *Juresania, Dictyoclostus, Marginifera, Reticulatia*), *Derbyia, Composita* (*Composita subtilita,* morphotypes S and O), chonetids (possibly *Lissochonetes, Neochonetes*), *Enteletes, Wellerella, Orbiculoidea, Petrocrania, Lingula,* and *Cleiothyridina* (arranged in approximate order of decreasing abundance).

Other studies (Cuffey, 1967; Newton, 1971; Lutz-Garihan and Cuffey, in press) included informal subdivision of the Wreford Megacyclothem into 22 successive stratigraphic horizons, each dominated by one or more particular rock types or lithofacies (abbreviations for which are presented in Table 1) in a particular geographic region. Table 2 indicates these horizons, which furnish the basic framework for consideration of Wreford brachiopod distributions. (For more detailed and precise representation of Wreford stratigraphy and *Composita* distribution, see Fig. 3.)

Figure 4 presents the distribution of each Wreford brachiopod group in the dominant lithofacies at each stratigraphic horizon in the different geographic areas within the Wreford outcrop belt. The various genera can be seen to occur in certain rock types, some genera in more rock

TABLE 1.—*Abbreviations for Rock Types Comprising Dominant Lithofacies at Various Wreford Horizons, and Used to Report Wreford Brachiopod Distributions.*

ABBREVIATION	ROCK TYPE
alg ls	algal limestone
alg-moll ls	algal-molluscan limestone
argill ls	argillaceous limestone
black sh	black shale
brach-moll ls	brachiopod-molluscan limestone
calc sh	calcareous shale
chlky ls	chalky limestone
chnl cgl	channel conglomerate
chty ls	cherty limestone
coal	coal
grn sh	green shale
gr-yl mud	gray-yellow mudstone
int brecc	intraformational breccia
moll ls	molluscan limestone
red sh	red shale
red ss	red channel sandstone
resid cl	red residual clay
tan ss	tan quartzose sandstone

TABLE 2.—*Abbreviations for Stratigraphic Horizons Recognized within the Wreford Megacyclothem and Used to Record Wreford Brachiopod Distributions.*

ABBREVIATION	STRATIGRAPHIC HORIZON				
mMw			middle part	of Wymore Shale Member	of Matfield Shale
lMw			lower part		
uWs			upper part	of Schroyer Limestone Member	of Wreford Limestone
umWs		upper beds	of middle part		
lmWs		lower beds			
lWs			lower part		
uuWh		upper beds	of upper part	of Havensville Shale Member	
luWh		lower beds			
mWh			middle part		
ulWh		upper beds	of lower part		
ullWh	upper portion	of lower beds			
lllWh	lower portion				
uuWt		upper beds	of upper part	of Threemile Limestone Member	
muWt		middle beds			
luWt		lower beds			
mWt			middle part		
lWt			lower part		
uuSp		upper beds	of upper part		of Speiser Shale
muSp		middle beds			
uluSp	upper portion	of lower beds			
lluSp	lower portion				
mSp			middle part		

types than others. The figure also shows that some genera have a more restricted geographic distribution than others.

Composita, productids, and *Derbyia* are the dominant brachiopods in the Wreford and are abundant and widely distributed. Occasionally, productid spines are found in rocks that have few, if any, other fossils. This implies that the small, lightweight spines were washed in from other areas, rather than that the productids themselves lived there.

Chonetids are not as abundant or widely distributed as the other three groups; they do not range as far south in the Wreford horizons.

The remaining brachiopod genera are minor parts of the fauna in the Wreford Megacyclothem and are rather infrequent. The only occurrence of *Wellerella* in cherty limestone is in the lower beds of the Threemile Limestone Member, in northern and central Kansas. This *Wellerella* zone was also noted by Hattin (1957, p. 31), who thought the occurrence was valuable stratigraphically by indicating contemporaneous deposition for this unit; however, *Wellerella* might well indicate similar paleoecologic conditions, rather than only the same time of burial. The genus *Cleiothyridina*, although found in other Permian units, has not been reported previously as occurring in the Wreford Megacyclothem. However, I found very small specimens at a few Kansas Wreford localities.

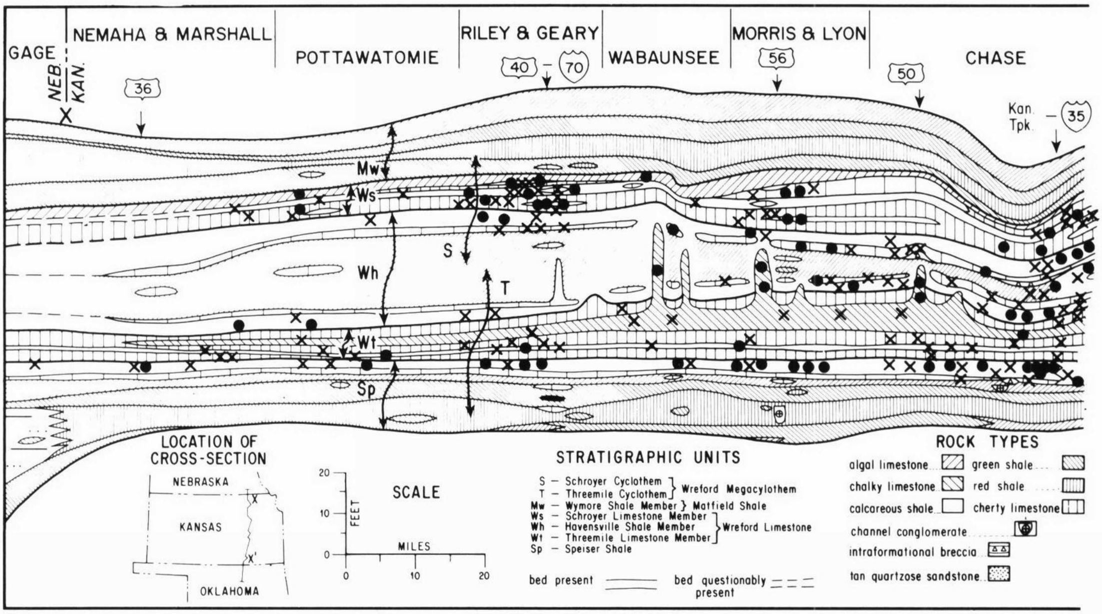

FIG. 3. Distribution and abundance of *Composita subtilita* in Wreford Megacyclothem.

PAST PRACTICES IN IDENTIFICATION OF SPECIES OF COMPOSITA

A literature search reveals several different schools of thought regarding the separation of various morphological forms of the genus *Composita* into species. As Grinnell and Andrews (1964, p. 233) report, *Composita* existed as a series of intergrading forms from the time of its first appearance in the Upper Devonian to its disappearance at the end of the Guadalupian. The fact that these apparently different forms intergrade morphologically at any given stratigraphic horizon has caused considerable problems in nomenclature. Some authors have recognized several different species (Girty, 1909; Weller, 1914; Dunbar and Condra, 1932; Brown, 1952; Chronic, 1953; Grinnell and Andrews, 1964; Sturgeon and Hoare, 1968; Stehli and Grant, 1970); some have placed all intergrading forms into one species (Hall and Clark, 1893; Sayre, 1930, 1931; Sutherland and Harlow, 1967); and others recognized morphotypes within one species (Burk, 1954; this paper).

MORPHOLOGIC VARIABILITY AND ITS IMPLICATIONS FOR IDENTIFICATION OF WREFORD COMPOSITA SUBTILITA

The Wreford *Composita* specimens constitute an intergrading series of individuals (Pl. 2, fig. 1-16) that cannot be separated into clearly distinct groups interpretable as separate species. Some specimens could be referred to *Composita subtilita,* whereas other specimens might well be classified as *Composita ovata.* Still other specimens might be placed in either species (both of which are recorded from Wolfcampian rocks, according to Grinnell and Andrews, 1964, p. 233) because they have some characteristics of each, or are intermediate in characteristics between the

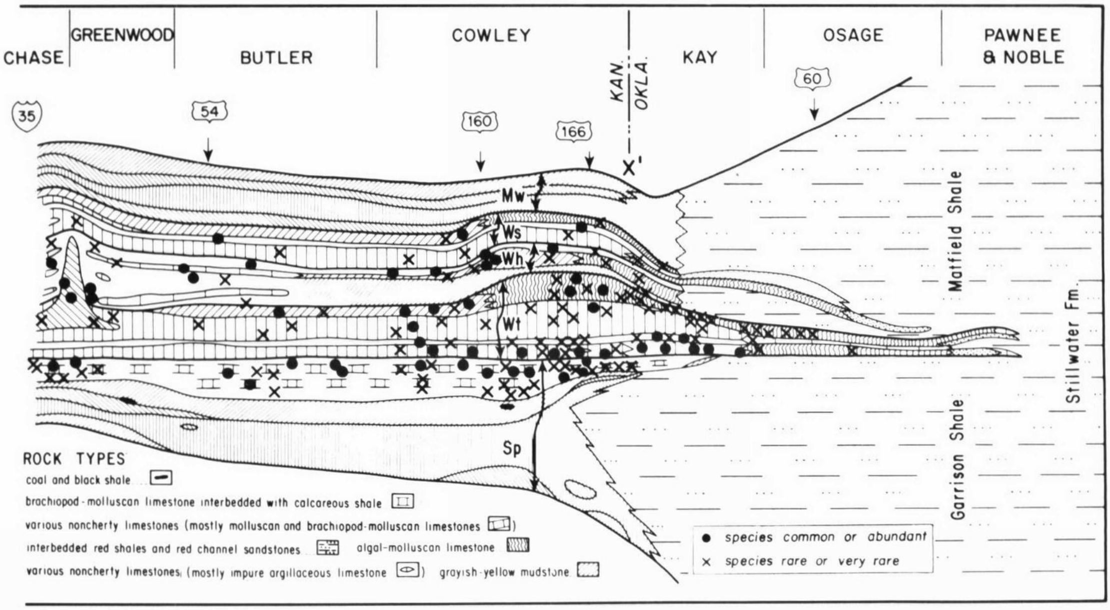

FIG. 3. *(Continued from facing page.)*

two. Appropriate plotting of measurements of well-preserved specimens (Garihan, 1973) indicates extensive overlap between these two nominal species, as well as the normal frequency distributions expected of a single biological species population (Cuffey, 1967, p. 35). All other collections of *Composita* reported in the literature, as discussed above, also apparently constitute intergrading populations.

Neontological species concepts should be kept in mind by practicing paleontologists, and applied wherever possible. These concepts were defined and discussed by Mayr (1963, p. 12-31; 1969, p. 23-36). Much previous reasoning about *Composita,* as for example by Weller (1914), seems not to have appreciated the potential relevance of biological concepts of species or of the use of specific names to identify populations of previously-living animals. Considerations like the usefulness of specific names as curatorial labels (Grinnell and Andrews, 1964, p. 242) or the desire to avoid trinomial names (Weller, 1914, p. 485-486) are clearly secondary to the necessity of understanding fossils as previously-living animal species.

A formal revision of all species within the genus *Composita* through time is far beyond the scope of this paper. From examination of the relevant literature, however, the genus at any one geological moment does appear to me likely to represent a single but highly variable species population that also changes morphologically through late Paleozoic time enough that segments of the evolving lineage could well be regarded as chronologically successive species.

In spite of the impracticability of a complete revision of *Composita,* neontological species concepts and their taxonomic consequences can be applied to Wreford *Composita.* As a result, all these fossils are here referred to the species *Composita subtilita.* Personal examination of the primary types of *Composita (Seminula) subtilita* and *Composita ovata* (in the Field Museum of Natural History, Chicago) indicates to me that both these type suites and the Wreford suite are so similar morphologically that all fall within the range of variation expectable for a single, highly variable, invertebrate species (Cuffey, 1967, p. 56, 59); I can find no consistently applicable criteria for separating these groups from one another at the species level. Thus, *Composita subtilita* (with which *Composita ovata* should now be synonymized) must be viewed as a stratigraphically long-ranging species, extending from

	northern Kansas and southernmost Nebraska	central Kansas	southern Kansas	southernmost Kansas and northernmost Oklahoma	northern Oklahoma
mMw	red sh	red sh	red sh	red sh	
lMw	grn sh	grn sh	grn sh	red sh	
uWs	alg ls CH	alg ls CDP	alg ls CD	alg-moll ls CDP	
umWs	chty ls CDP calc sh CDHPY	brach-moll ls CDPY	chty ls CDPY calc sh CDP	calc sh C	gr-yl mud D
lmWs	calc sh CDHPEO	calc sh CDHPO	calc sh CP	calc sh C	gr-yl mud D
lWs	chty ls CDP	chty ls CDHP	chty ls CHPO	chty ls CP	alg-moll ls CDP tan ss
uuWh	calc sh CDHP	calc sh CDHPO	calc sh CDP	calc sh CHP	
luWh	moll ls CDP	brach-moll ls CDP	alg ls CP	alg-moll ls CH	
mWh	gr-yl mud DP	gr-yl mud CDH calc sh CDHPO	gr-yl mud	brach-moll ls CP	
ulWh	moll ls CDHPE	brach-moll ls CDHPE	alg ls C	alg-moll ls CDP	alg-moll ls CDP moll ls
ullWh	calc sh CDHPE	calc sh CDHPO	alg ls C	alg-moll ls CDP	alg-moll ls CDP
lllWh	calc sh CDHPEOT	calc sh CDHP	alg ls CD	alg-moll ls CDP	alg-moll ls CP tan ss
uuWt	chty ls CDHP	chty ls CDHPO	chty ls CDHP	chty ls CDP	brach-moll ls
muWt	chlky ls C	chlky ls CDPEY	chty ls CDP	chty ls CDP	brach-moll ls
luWt	chty ls CDHPE	chty ls CDPE	chty ls CDP	chty ls DP	brach-moll ls CD
mWt	calc sh CDHPEO	calc sh CDHPEW	calc sh CDHPE	calc sh CDHPE	brach-moll ls CD
lWt	chty ls CDHPEW	chty ls CDHPEW	chty ls CDHPEY	brach-moll ls CDHP	alg-moll ls CP tan ss moll ls
uuSp	calc sh CDHPEWOT	calc sh CDHPEWOTL	calc sh CDHPEWOL brach-moll ls CDHPWO	calc sh CDP brach-moll ls CDP	
muSp	moll ls DHP	moll ls CDPHE	calc sh CDHPWOL brach-moll ls CDHPO	gr-yl mud DP	
uluSp	gr-yl mud	gr-yl mud DP	gr-yl mud DPO		
lluSp	grn sh HP (spines)	grn sh D	gr-yl mud		
mSp	red sh	red sh	red sh		

(ruled pattern indicates interbedded red shale and red sandstone)

FIG. 4. Distribution of Wreford brachiopod groups; symbols denoting presence of particular group in indicated rock type at indicated horizon in indicated region are *C, Composita; D, Derbyia; H,* chonetids; *P,* productids; *E, Enteletes; W, Wellerella; O, Orbiculoidea; T, Petrocrania; L, Lingula; Y, Cleiothyridina* (rock type abbreviations from Table 1, and stratigraphic horizon abbreviations from Table 2).

latest Mississippian or earliest Pennsylvanian time well into Early Permian time, a time span comparable to that through which at least some Cenozoic invertebrate species have endured.

As stated previously, the Wreford suite can be viewed as a continuous intergradation between two species as end members. These two cannot be regarded as subspecies because subspecies are geographically separate groups (Mayr, 1969, p. 41), and these two end members occur together in single samples of *Composita subtilita* collected from individual localities. Moreover, for the same reason, the two end members are clearly not stratigraphically separated segments of a continuously evolving lineage. They are found in the same sedimentary environments, so they cannot be explained as two ecotypes. Nor can they be sexual dimorphs, because there is too much continuous intergradation morphologically. These two end members should be regarded as morphotypes, like those in *Tabulipora carbonaria* of the Wreford (Cuffey, 1967, p. 61-63). However, nomenclatural designation of these morphotypes poses problems. Although some workers (Grinnell and Andrews, 1964, p. 243) preferred not to change *Composita* species-level terminology, doing so seems the only practical way for our increased paleobiologic understanding of *Composita* populations to be reflected taxonomically. The two end members could be labelled as varieties of the single species, except that varieties no longer have status in modern biological nomenclature. Or, they could be designated as morphotypes subtilita and ovata (not italicized), but retention of the originally Latinized name even informally is potentially confusing. Consequently, I have labelled them as morphotypes "S" and "O" of *Composita subtilita,* the letters maintaining an obvious linkage with previous and familiar typological practices.

SYSTEMATIC PALEONTOLOGY

Phylum BRACHIOPODA Duméril, 1806

Class ARTICULATA Huxley, 1869

Order SPIRIFERIDA Waagen, 1883

Suborder ATHYRIDIDINA Boucot, Johnson, and Staton, 1964

Superfamily ATHYRIDACEA M'Coy, 1844

Family ATHYRIDIDAE M'Coy, 1844

Subfamily ATHYRIDINAE M'Coy, 1844

Genus COMPOSITA Brown, 1849

COMPOSITA SUBTILITA (Hall, 1852)

Plates 1, 2

Synonymy.—Extensive literature search revealed only one reference (Sayre, 1931) not listed in previous synonymic indexes. Consequently, the reader is referred to the comprehensive synonymies for *Composita subtilita* contained in such indexes (Schuchert, 1897; Weller, 1898; Girty, 1915; Branson, 1948; Carter and Carter, 1968).

Shell morphology.—Shell smooth, globular, or lens shaped, exterior marked by concentric growth lines. Pedicle valve pierced by oval foramen; anterior margin displaying dorsal fold and ventral sulcus in mature specimens, but not in many immature forms.

Shell small to medium sized, moderately biconvex, dimensions highly variable, but *GL, GW,* and *GT* averaging about 17 mm, 15 mm, and 10 mm, respectively. (Table 3 gives values for these and other numerical characteristics.) Shell, when viewed perpendicularly to plane of commissure, oval to round or subquadrate in outline; width-length ratio *(GW/GL)* averaging about 0.9.

TABLE 3.—*Tabulation of Measured Characters for 782 Measured Specimens of* Composita subtilita *from the Wreford Megacyclothem.* (N=number of specimens; $\bar{X}$=mean; CL=confidence limit; SD=standard deviation; CV=coefficient of variability; FSA, PLMA, and ALMA in degrees; all others in mm.)

	N	$\bar{X}$ 95% CL	$\bar{X}$	SD 95% CL	SD	RANGE	CV%
GL	482	16.35- 17.99	17.17	8.99- 9.85	9.23	2.2- 40.1	53.74
GW	430	13.99- 15.55	14.77	7.94- 8.76	8.20	1.9- 36.2	55.51
GT	233	9.45- 10.93	10.19	5.37- 6.46	5.86	1.2- 23.4	57.51
LPGW	361	8.94- 10.12	9.53	5.26- 6.08	5.62	1.1- 26.4	58.99
LPGT	217	7.00- 8.14	7.57	3.95- 4.78	4.33	0.9- 16.4	57.12
POGL	395	1.69- 1.81	1.75	0.60- 0.69	0.64	0.3- 3.9	36.72
POGW	389	1.25- 1.33	1.29	0.42- 0.48	0.45	0.2- 2.9	35.03
FSA	148	145.82-154.96	150.39	25.49-32.09	28.35	95.0-180.0	18.85
PLMA	157	87.50- 90.56	89.03	8.78-11.01	9.78	52.0-158.0	10.98
ALMA	58	82.47- 88.19	85.33	9.20-13.38	10.86	58.0-107.0	12.72
FSHA	163	2.11- 3.01	2.563	2.59- 3.23	2.876	0.0- 9.8	112.2

TABLE 4.—*Summary of Ratios Calculated from Measurements of Wreford* Composita subtilita *Specimens.* (Symbolization as for Table 3.)

RATIO	$\bar{X}$	SD	RANGE	N
GW/GL	0.91	0.08	0.69-1.10	321
GT/GW	0.66	0.10	0.42-0.96	176
LPGW/GL	0.60	0.06	0.37-0.92	308
LPGT/GL	0.45	0.05	0.32-0.61	188
FSHA/GT	0.33	0.10	0.08-0.57	55

(Table 4 summarizes ratio data.) Valves biconvex, mean convexity *(GT/GW)* approximately 0.7. Greatest width of shell in many specimens anterior to midpoint of shell but in others at midpoint or posterior to midpoint; *LPGW* averaging about 10 mm; ratio of length position of greatest width to shell length *(LPGW/GL)* averaging about 0.6. Greatest thickness at midpoint or posterior to midpoint of shell length, but in some anterior to midpoint; *LPGT* averaging about 8 mm; ratio of length position of greatest thickness to shell length *(LPGT/GL)* averaging about 0.5. Hinge line short. Beak of pedicle valve curving around beak of brachial valve. Anterior margin of shell marked by dorsal fold and ventral sulcus, of height *(FSHA)* varying from 0 to 9.8 mm but averaging about 2.6 mm; *relative* fold and sulcus height (ratio of height in mm to greatest shell thickness, *FSHA/GT*) ranging from 0.08 to 0.57 but averaging near 0.3; in shells with fold and sulcus developed, fold and sulcus angle *(FSA)* averaging about 150°; fold and sulcus begin at varying distances from the posterior end. Posterolateral margins of shell forming angle *(PLMA)* varying from 52° to about 160° but averaging approximately 90°. Anterolateral margin angle *(ALMA)* mean approximately 85°.

Pedicle valve most convex at apex, gradually sloping off to shell margins. Pedicle opening an oval foramen at beak of valve; opening averaging about 1.3 mm wide *(POGW)* by 1.8 mm long *(POGL)*; delthyrium (triangular open space below foramen) covered by brachial valve. A few pedicle valves bearing shallow median groove beginning at or slightly anterior to apex and continuing to anterior commissure.

Brachial valve most convex posterior to midlength and curving more gradually from there to shell margins.

Pedicle valve interior bearing two hinge teeth supported by dental lamellae extending to floor (interior surface) of valve. Muscle scars elongate, causing thinning of shell. Deep channel in middle of shell near posterior end for pedicle muscles (Dunbar and Condra, 1932, p. 364). Mantle canals of one specimen showing a simple bifurcating pattern (described below).

Brachial valve interior with two sockets on either side of a quadrate hinge plate. Adductor scars long and narrow. Previous workers (Boucot *et al.*, 1965, p. *H*662) have described brachidia: jugal saddle present; jugal bifurcations terminating between first and second volutions of spiralia. Spiralia laterally directed.

Exterior surface of valves smooth except for irregularly spaced growth lines, which become more prominent toward anterior.

Dimensions of several specimens are presented in Table 5.

Mantle canals.—Mantle canals are visible on one specimen of *Composita subtilita,* in which the shell material has been partly broken away to leave an internal mold showing the mantle canals as ridges. The pattern formed by these mantle canals (Fig. 5; Pl. 1, fig. 12,13) closely resembles that described by Weller (1931, p. 355-357).

Brachidia.—Weller (1931) discussed the position of the lophophore-bearing spires within shells of *Composita subtilita.* He noted their attachment by short delicate crura, which were broken in almost all specimens, so that the brachidia were free to move around in the shell and were thus fossilized in various positions.

Although many of the *Composita subtilita* studied still contain brachidia, even in crushed specimens, and some of them appear to be still in life position with the spires directed laterally (Pl. 2, fig. 17), thus far no brachidia have been observed attached directly to the crura. Acetate peels made from several other specimens reveal that the brachidia within have been moved variously from their life position (Pl. 2, fig. 18).

Morphotypes.—As discussed previously, two distinct morphotypes occur within the Wreford population of *Composita subtilita:*

TABLE 5.—*Dimensions of Some Specimens of Wreford* Composita subtilita, *and Dimensions of the Holotype of* Composita ovata *and the Lectotype of* Composita subtilita.

SPECIMEN	GL (mm)	GW (mm)	GT (mm)	LPGW (mm)	LPGT (mm)	POGL (mm)	POGW (mm)	FSA (degrees)	PLMA (degrees)	ALMA (degrees)	FSHA (mm)
CH16E-p-01	30.4	25.6	18.9	17.8	14.3	2.6	1.7	116.0	82.0	77.0	7.9
BU04I-p-03	19.3	17.7	10.4	10.9	8.3	1.7	1.1	149.0	90.0	95.0	1.8
CY49A-p-13	24.2	22.6	16.0	14.4	11.9	1.8	1.5	123.0	99.0	86.0	5.1
KA0IJ-f1-08	23.0	19.6	13.4	13.6	8.8	2.0	1.7	135.0	93.0	91.0	4.2
KA08A-f1-10	25.8	22.5	17.4	16.9	13.3	2.7	2.0	127.0	81.0	58.0	4.4
holotype of *Composita ovata*	27.0	26.8	13.8	16.5	11.4	2.5	1.9	134.0	80.0	95.0	3.1
lectotype of *Composita subtilita*	20.7	17.9	13.8	12.1	9.6	2.3	1.7	122.0	76.0	81.0	4.4

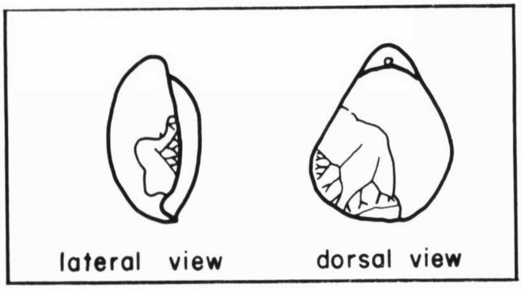

FIG. 5. Mantle canals of *Composita subtilita;* diagrammatic sketch of Wreford specimen CH22H-p-01 with portions of the shell broken away to show an internal mold of the mantle canals; drawing of lateral view does not show mantle canals present on the brachial valve.

Composita subtilita morphotype S

Plate 1, figures 1-4

Morphotype (the narrow typological concept *"Composita subtilita"* (Hall, 1852)) similar to species; differs by being relatively elongate, with a low width/length ratio (that is, length noticeably greater than width, *GW/GL* averaging about 0.8). The anterior line of commissure varies from uniplicate to parasulcate. The fold and sulcus are high, both absolutely (*FSHA* averaging about 6 mm) and relatively (*FSHA/GT* averaging near 0.4). Summary statistics for the ratios of this variety are given in Table 6.

TABLE 6.—*Summary of Ratios Calculated from Measurements of Wreford* Composita subtilita *Morphotype S.* (Symbolization as for Table 3.)

RATIO	$\bar{X}$	SD	RANGE	N
GW/GL	0.83	0.05	0.70-0.95	32
FSHA/GT	0.37	0.08	0.19-0.57	32

Composita subtilita morphotype O

Plate 1, figures 5-8

Morphotype (the narrow typological concept *"Composita ovata"* Mather, 1915) similar to species; differs by having a rounded outline, with a comparatively high width/length ratio (*GW/GL* averaging about 0.9), and length and width about the same. The anterior line of commissure is uniplicate. The fold and sulcus are low, both absolutely (*FSHA* averaging about 4 mm) and relatively (*FSHA/GT* averaging near 0.3). Summary statistics for ratios of this variety are indicated in Table 7.

TABLE 7.—*Summary of Ratios Calculated from Measurements of Wreford* Composita subtilita *Morphotype O.* (Symbolization as for Table 3.)

RATIO	$\bar{X}$	SD	RANGE	N
GW/GL	0.92	0.07	0.85-1.11	27
FSHA/GT	0.26	0.10	0.08-0.50	23

Stratigraphic distribution.—The oldest specimens of *Composita subtilita* are from earliest Pennsylvanian (Grinnell and Andrews, 1964, p. 235) or latest Mississippian rocks (Boucot *et al.*, 1965, p. *H*662), and the youngest are found in the Leonardian Series of the Permian. All of these specimens are similar in external morphology. Moreover, within the Wreford population at least, *Composita subtilita* does not show any microevolutionary variability.

CAUSES OF MORPHOLOGIC VARIABILITY

CONSIDERATION OF MORPHOTYPES

The two morphotypes of *Composita subtilita* were found to be discouragingly similar, and thus the previous descriptions are quite brief. Also, the two morphotypes occurred in approximately equal numbers in the different Wreford rock types, stratigraphic horizons, and geographic regions. To obtain better numerical characterization of the two morphotypes, a subsample of 74 well-preserved and full-sized specimens was selected. It included 40 specimens referable to *Composita subtilita* morphotype S and 34 specimens referable to *Composita subtilita* morphotype O. Some of these specimens were easily placed in one group or the other, but many were intermediate in their external characteristics and could only be placed more or less arbitrarily. Summary statistics for the data taken from this subsample were then calculated (Tables 8 and 9).

For each morphological characteristic, t-tests for comparing the means of the two morphotypes show statistically significant differences between the morphotypes in some characters but not others. However, where the means of numerical characters do differ significantly, the small differences in their absolute values effectively prevent any conclusions regarding biologic significance.

Statistics were also calculated for each character from all measurable Wreford specimens of

TABLE 8.—*Tabulation of Measured Characters of Well-preserved Full-sized Wreford* Composita subtilita *Morphotype S Specimens.* (Symbolization as for Table 3.)

	N	$\bar{X}$ 95% CL	$\bar{X}$	SD 95% CL	SD	RANGE	CV%
GL	40	23.96- 26.16	25.06	2.84- 4.48	3.45	18.0- 31.7	13.79
GW	37	19.58- 21.74	20.66	2.68- 4.29	3.27	12.2- 26.7	15.83
GT	36	15.90- 17.66	16.78	2.13- 3.45	2.61	10.4- 21.2	15.60
LPGW	35	14.50- 16.04	15.27	1.84- 2.99	2.26	10.0- 19.6	14.81
LPGT	35	11.39- 12.73	12.06	1.61- 2.62	1.98	8.3- 16.4	16.47
POGL	16	2.12- 2.44	2.28	0.22- 0.46	0.30	1.7- 2.7	13.18
POGW	15	1.45- 1.79	1.62	0.23- 0.49	0.31	1.1- 2.0	18.60
FSA	31	110.61-117.85	114.23	7.86-13.15	9.84	95.0-140.0	8.59
PLMA	32	80.35- 86.09	83.22	6.37-16.00	7.95	60.0- 94.0	9.53
ALMA	31	78.28- 86.10	82.19	8.51-14.24	10.65	58.0- 97.0	12.98
FSHA	37	5.31- 6.53	5.92	1.49- 2.39	1.82	1.5- 8.6	30.60

TABLE 9.—*Tabulation of Measured Characters of Well-preserved Full-sized Wreford* Composita subtilita *Morphotype O Specimens.* (Symbolization as for Table 3.)

	N	$\bar{X}$ 95% CL	$\bar{X}$	SD 95% CL	SD	RANGE	CV%
GL	31	22.37- 24.81	23.59	2.69- 4.50	3.37	17.2- 31.4	14.25
GW	32	20.75- 23.09	21.92	2.62- 4.35	3.26	17.0- 29.5	14.92
GT	27	13.43- 15.73	14.58	2.22- 3.86	2.81	9.9- 21.0	19.39
LPGW	31	13.53- 15.13	14.33	1.73- 2.89	2.17	10.6- 18.9	15.17
LPGT	26	10.11- 11.75	10.93	1.59- 2.80	2.02	7.5- 15.7	18.37
POGL	20	1.90- 2.30	2.10	0.33- 0.63	0.43	1.5- 2.9	20.49
POGW	21	1.42- 1.68	1.55	0.13- 0.40	0.28	1.0- 2.0	18.05
FSA	25	127.71-139.89	133.80	11.54-20.59	14.78	97.0-161.0	11.03
PLMA	29	90.53- 93.89	92.21	3.51- 5.98	4.42	82.0-102.0	4.79
ALMA	18	85.76- 91.80	88.78	4.58- 9.14	6.10	77.0- 98.0	6.88
FSHA	25	3.32- 5.10	4.21	1.77- 3.16	2.27	1.0- 9.4	53.90

Composita subtilita (Table 3). This summary, therefore, includes measurements taken on many smaller specimens (on the order of 5 mm in length) as well as on full-sized ones. Consequently, many character means for the Wreford population as a whole (Table 3) are somewhat lower than the mean values for the morphotypes, as calculated from the well-preserved full-sized specimens of the subsample (Tables 8 and 9).

The shape of specimens of *Composita subtilita* from the Wreford is rounded or elongate, the convexity is high or low, and the line of commissure along the anterior portion of the valves is parasulcate, uniplicate and low, or uniplicate and high. These character states can be combined in 12 possible ways. The Wreford population of *Composita subtilita* includes individuals matching each of these combinations, underscoring the failure of any single character to adequately differentiate the morphotypes, and strengthening the conclusion that the two end members in fact represent morphotypes.

CONSIDERATION OF ENTIRE POPULATION

All specimens regardless of morphotype which were collected from particular rock types, stratigraphic horizons, or geographic areas were grouped together, and the morphologic characteristics of each such group were summarized statistically and graphically.

In order to discover whether any differences exist among specimens of *Composita subtilita* from the various Wreford rock types, plots of character means calculated for all specimens from each rock type were drawn. Figure 6 summarizes the means for *GT* for *Composita subtilita* from different rock types. This and similar plots (values contained in Garihan, 1973, p. 203-209) show no trends or large differences in the means. Thus, *Composita subtilita* did not vary morphologically among any of the various rock types in which it was found.

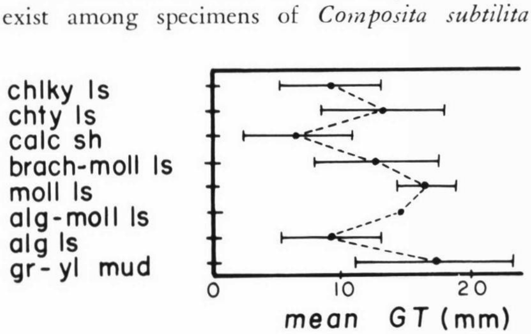

FIG. 6. Ecologic variation in the character *GT*, greatest thickness of shell (dot indicates mean, bar extends one standard deviation on each side), for *Composita subtilita* specimens from different rock types of the Wreford (arranged approximately according to transgressive cyclic order); rock type abbreviations are from Table 1.

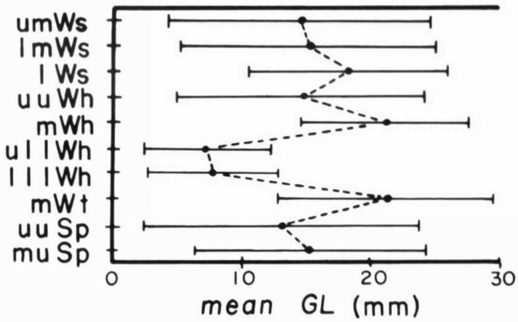

FIG. 7. Evolutionary (stratigraphic) variation in the character *GL*, greatest length of shell (dot indicates mean, bar extends one standard deviation on each side), for *Composita subtilita* specimens from various calcareous shale horizons of the Wreford; horizon abbreviations are from Table 2.

For the groups of specimens obtained from the various stratigraphic horizons dominated by calcareous shales, similar plots were made. These plots are also ambiguous in that they show no trends in the data for any of the eleven characters (Fig. 7 summarizes this information for *GL*; Garihan, 1973, p. 210-216, presented the data). Plots were also made for specimens of *Composita subtilita* from cherty limestone horizons and from brachiopod-molluscan limestone horizons, and again no trends emerged (Garihan, 1973, p. 217-225). Thus, there is no noticeable evolutionary change in successive populations of *Composita subtilita* in the Wreford Megacyclothem.

In a similar manner, the means of the several characters were compared for groups of specimens from several localities in the upper Speiser calcareous shale. Figure 8 presents this information for *GW* (also see Garihan, 1973, p. 226-230). These plots do not indicate any systematic variation geographically.

In summary, neither consideration of morpho-

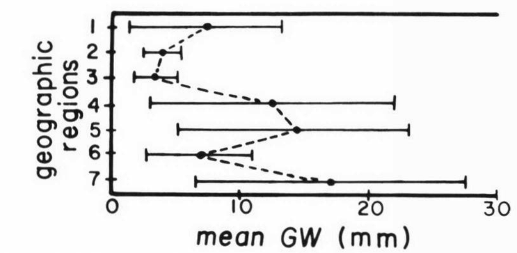

FIG. 8. Clinal (geographic) variation in the character *GW*, greatest width of shell (dot indicates mean, bar extends one standard deviation on each side), for Wreford *Composita subtilita* specimens from the widespread calcareous shale of the upper part of the upper Speiser. Geographic regions are: 1) Gage Co., Neb.; Marshall and northern Pottawatomie Cos., Kans.; 2) southern Pottawatomie, Riley, and Geary Cos. Kans.; 3) Wabaunsee, Morris, and Lyon Cos., Kans.; 4) northern Chase Co., Kans.; 5) southern Chase and Greenwood Cos., Kans.; 6) Butler Co., Kans.; 7) Cowley Co., Kans.; Kay, Osage, Pawnee, and Noble Cos., Okla.

types nor examination of the entire species population shows any systematic variations which can be interpreted ecologically, evolutionarily, or clinally.

DISTRIBUTION, ABUNDANCE, AND PALEOECOLOGY

Composita subtilita can be collected in large numbers from some of the well-understood lithologic facies within the Wreford Megacyclothem; therefore, variations in the distributional abundance of this species may yield an understanding of its paleoautecology.

Composita subtilita is found abundantly in calcareous shale and brachiopod-molluscan limestone, and commonly in cherty limestone, of the Wreford Megacyclothem (Figure 3). Other rock types containing a few individuals of this species are chalky limestone, algal-molluscan limestone, algal limestone, and molluscan limestone. Because *Composita subtilita* existed throughout the time of deposition of the Wreford and ranged geographically throughout the Mid-Continent, its distribution (presence or absence) in particular rock types must reflect dependence on the conditions of the environments of deposition. Thus, *Composita subtilita* occurs in large numbers in normal marine calcareous shale and brachiopod-molluscan (and even cherty) limestone, but only in small numbers in other rocks formed in water which may have been slightly more brackish than normal marine (molluscan limestone), or possibly even slightly hypersaline(algal limestone). This species is not found in rocks which were probably brackish, nor in predominantly detrital terrigenous rocks. Thus, salinity and sediment supply seem most important as limiting factors for the distribution of *Composita subtilita;* this species could not tolerate differences much above or below normal marine salinity or localities with a large terrigenous sediment supply that would smother them. The occurrence of *Composita subtilita* only at the southern end of some molluscan limestone beds implies that the properties of the water varied somewhat even within the depositional area of a single rock type, by being too brackish or too sediment-laden farther north for survival of *Composita subtilita.* Depth seems unimportant as a limiting factor, inasmuch as the species is found in some rocks previously interpreted as deep-water deposits (cherty limestone), and in other rocks interpreted as shallow-water deposits (algal limestone) in the Wreford sea (Cuffey, 1967; Newton, 1971).

Referring again to Figure 3, specimens of *Composita subtilita* from the uppermost Speiser and lowermost Threemile horizons become more abundant to the south; this trend is particularly noticeable in field collecting around the Kansas-Oklahoma border. Because this trend is not seen in other horizons, it seems likely that the southern part of the Wreford belt at that time was an area with extensive shell beds covering the floor of the Wreford sea. *Derbyia* sp. is also abundant along with *Composita subtilita.*

Two calcareous shale horizons yielded large numbers of very small specimens of *Composita subtilita;* this "dwarfed" fauna might indicate that conditions had become unfavorable for survival of this species to fully adult maturity. However, a few large specimens are found there as well. There was no accompanying evidence of mass mortality of all forms at these horizons, so it seems unlikely that this occurrence results from drastic changes in the environment, such as water-quality changes or a large influx of sediment. Perhaps the large number of small specimens of this species simply indicates insufficient food resources to support such a large number of immature individuals until maturity.

SUMMARY AND CONCLUSIONS

1) Collections of brachiopods from the Lower Permian Wreford Megacyclothem in Nebraska, Kansas, and Oklahoma include large numbers of well-preserved specimens of *Composita.*

2) Other widespread and abundant Wreford brachiopod groups include *Derbyia* and productids, with chonetids being somewhat less abundant and widely distributed. Minor brachiopod groups are *Lingula, Orbiculoidea, Petrocrania, Enteletes, Wellerella,* and *Cleiothyridina* (not previously reported from the Wreford).

3) Various standard techniques were employed to investigate the Wreford specimens of *Composita.* In addition, eleven numerical characters were defined and measured on each well-preserved specimen, thus generating quantitative data for a better understanding of the paleobiology of this species.

4) At any one stratigraphic horizon of the Wreford, the genus *Composita* is composed of two morphologically distinct forms, which have been treated by some previous workers as separate species, and as varieties of one species by others. The *Composita* population comprises an intergradational series of individuals not clearly separable into distinct species. Thus, the two morphological end members of this continuously intergradational series are here treated as morphotypes of a single species, named *Composita subtilita* morphotype S, and *Composita subtilita* morphotype O. In the Wreford population, then, the two species *Composita subtilita* and *Composita ovata* are regarded as synonyms.

5) Systematic descriptions of Wreford *Composita subtilita* and its morphotypes, including summaries of numerical data, are given.

6) Analysis of the numerical characteristics of subsamples consisting of well-preserved, full-sized specimens of both morphotypes shows statistically significant differences between the morphotypes in some characters but not in others. The small difference in absolute values of these characters, however, prevents biologically meaningful explanations of these statistical differences. Moreover, the two morphotypes do not differ as to their distribution and abundance in different Wreford rock types, stratigraphic horizons, or geographic regions. Thus, the morphotypes cannot be explained as ecotypes, evolutionary populations, geographic subspecies, or sexual dimorphs, and they can only be regarded as intraspecific morphotypes.

7) Morphologic (especially numerical) characteristics of the entire Wreford *Composita subtilita* population were considered in order to determine whether differences due to paleoecological (lithologic), evolutionary (stratigraphic), or clinal (geographic) causes exist; however, none appear to be present.

8) The distribution and abundance of *Composita subtilita* in the Wreford Megacyclothem in particular rock types presumably reflects dependence on the environmental conditions of deposition producing those rock types. The occurrence of this species in various rock types suggests that salinity and sediment influx may have been its principal limiting environmental factors.

9) A trend toward increasing abundance of *Composita subtilita* to the south in the uppermost Speiser and lowermost Threemile implies that extensive shell beds briefly covered the floor of the Wreford sea in the southern part of its area of distribution.

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ADDENDUM

SPECIMEN NUMBER EXPLANATION

The first 4 characters refer to localities; for example, BU04 refers to outcrop 4 in Butler County, Kansas. Precise locations of these outcrops are given in either Cuffey (1967), Newton (1971), or this paper (p. 4). The next letter or series of letters refers to a particular bed within the outcrop. In turn, symbols *fl* and *p* refer to the method of collecting: *fl,* sample picked from float; *p,* sample picked in place from the surface of the particular bed. The final number is that assigned to a brachiopod specimen from the sample under consideration. This is the standard labeling procedure developed for Wreford collections and has previously been used for bryozoan studies.

For the figured brachiopod specimens of Plates 1 and 2, the rock type, stratigraphic horizon, and collection locality are listed below.

BU04P: calcareous shale, middle Schroyer, Loc. BU04

CH16E: molluscan limestone, upper Speiser, Loc. CH16

CH18L: calcareous shale, upper Speiser, Loc. CH18

CH22H: brachiopod-molluscan limestone, upper Havensville, Loc. CH22

CH33D: calcareous shale, upper Speiser, Loc. CH33

CY04Cm3: middle third of cherty limestone, upper Threemile, Loc. CY04
CY20Ha: algal limestone, upper Havensville, Loc. CY20
CY37Jb: brachiopod-molluscan limestone, upper Speiser, Loc. CY37
CY46C: calcareous shale, upper Speiser, Loc. CY46
CY49B&A: brachiopod-molluscan limestone, lower Threemile, Loc. CY49
CY100A: unknown locality, Cowley Co., Kansas
GR01P: cherty limestone, lower Schroyer, Loc. GR01
KA01J: brachiopod-molluscan limestone, lower Threemile, Loc. KA01
KA08A: brachiopod-molluscan limestone, lower Threemile, Loc. KA08
ML01D: calcareous shale, upper Speiser, Loc. ML01

EXPLANATION OF PLATES

(Figured and cited specimens are housed in the Paleobryozoological Research Collection, Department of Geosciences, The Pennsylvania State University.)

PLATE 1

Composita subtilita from the Wreford Megacyclothem of Nebraska, Kansas and Oklahoma.

FIGURE

1-4. *Composita subtilita* morphotype S; *1*, dorsal view; *2*, ventral view; *3*, lateral view; *4*, anterior view; specimen slightly asymmetrical from uneven growth; specimen KA08A-f1-04 (all × 1).

5-8. *Composita subtilita* morphotype O; *5*, dorsal view; *6*, ventral view; *7*, lateral view; *8*, anterior view; specimen CH33D-fl-31 (all × 1).

9. Interior of pedicle valve showing oval pedicle opening (foramen), triangular delthyrium below pedicle opening, and hinge teeth, specimen CH33D-fl-03 (× 3).

10. Interior of brachial valve, showing subquadrate hinge plate, specimen CH33D-fl-07 (× 3.5).

11. Interior view of brachial valve of another specimen, showing hinge plate and elongate adductor muscle scars, specimen ML01D-fl-05 (× 3.5).

12,13. Specimen showing internal mold of mantle canals; *12*, oblique view of brachial valve (× 2); *13*, lateral view (× 2.3); specimen CH22H-p-01.

14. Interior of pedicle valve showing elongate adductor muscle scars and deep channel for pedicle muscles near pedicle opening, specimen CH33D-fl-06 (× 2).

PLATE 2

Composita subtilita from the Wreford Megacyclothem of Nebraska, Kansas, and Oklahoma. (× 1 unless otherwise indicated.)

FIGURE

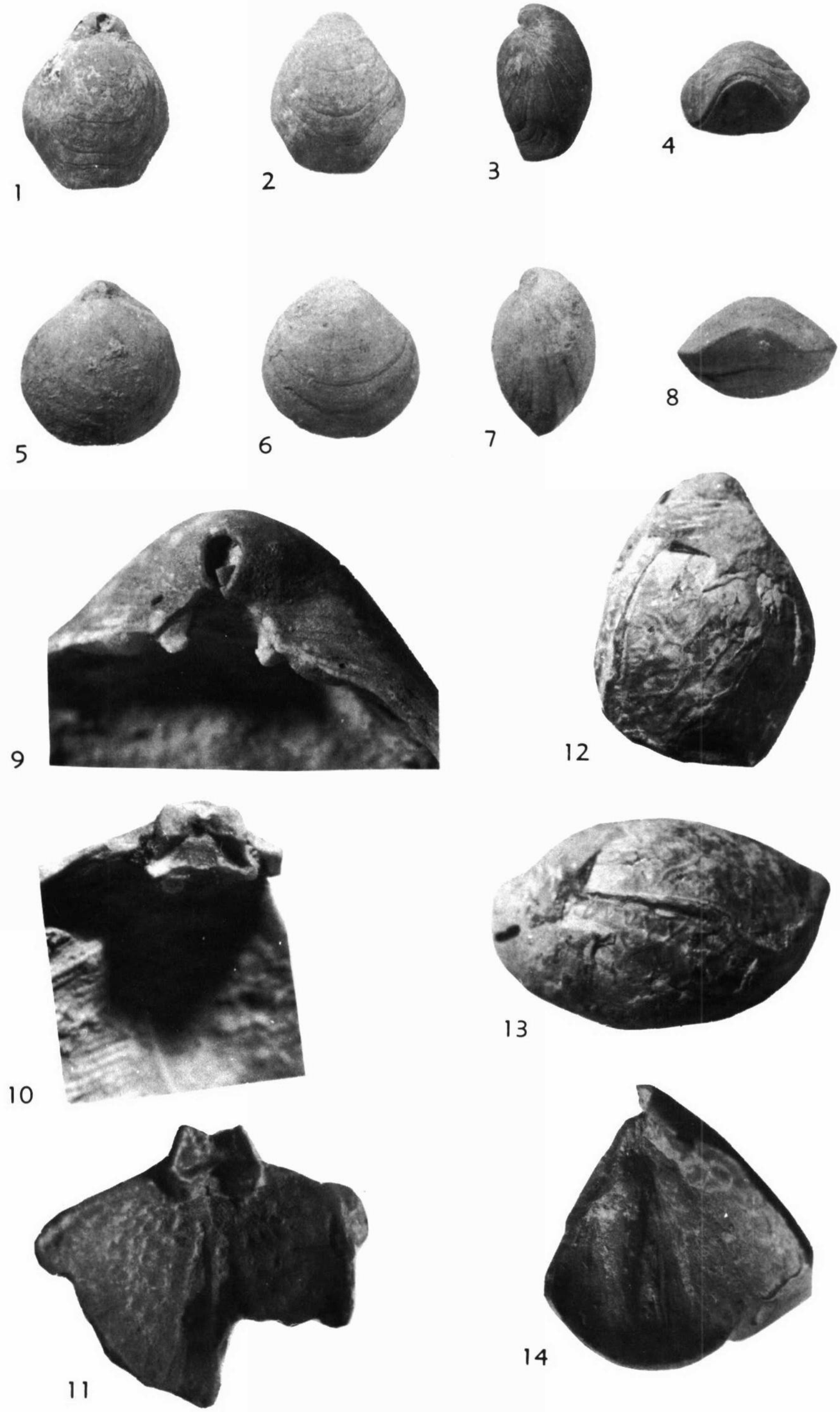
1-5. Series of specimens showing a gradual increase in convexity of both valves from lens shaped *(1)* to globular *(5)*; specimens: *1*, BU04P-p-03; *2*, CY20Ha-p-02; *3*, KA01J-fl-03; *4*, CY46C-p-01; *5*, KA01J-fl-05.

6-10. Series of specimens showing a gradual increase in fold and sulcus height from very low *(6)* to very high *(10)*; specimens: *6*, CH18L-fl-01; *7*, KA01J-fl-01; *8*, KA08A-fl-01; *9*, GR01P-p-02; *10*, KA01J-fl-09.

11-16. Series of specimens showing a gradual change in shape from elongate (length greater than width) *(11)* to round *(15)* and elongate (width greater than length) *(16)*; specimens: *11*, KA01J-fl-05; *12*, CY37Jb-p-02; *13*, KA01J-fl-19; *14*, CH16E-p-02; *15*, KA01J-fl-18; *16*, CY49B&A-fl-21.

17. Specimen with outer part of shell eroded away, revealing laterally directed spiralia, probably in place, specimen CY04Cm3-p-01 (× 2).

18. Peel photograph, showing broken spiralia; left spiral is within right spiral, specimen CY100A-p-01 (× 2).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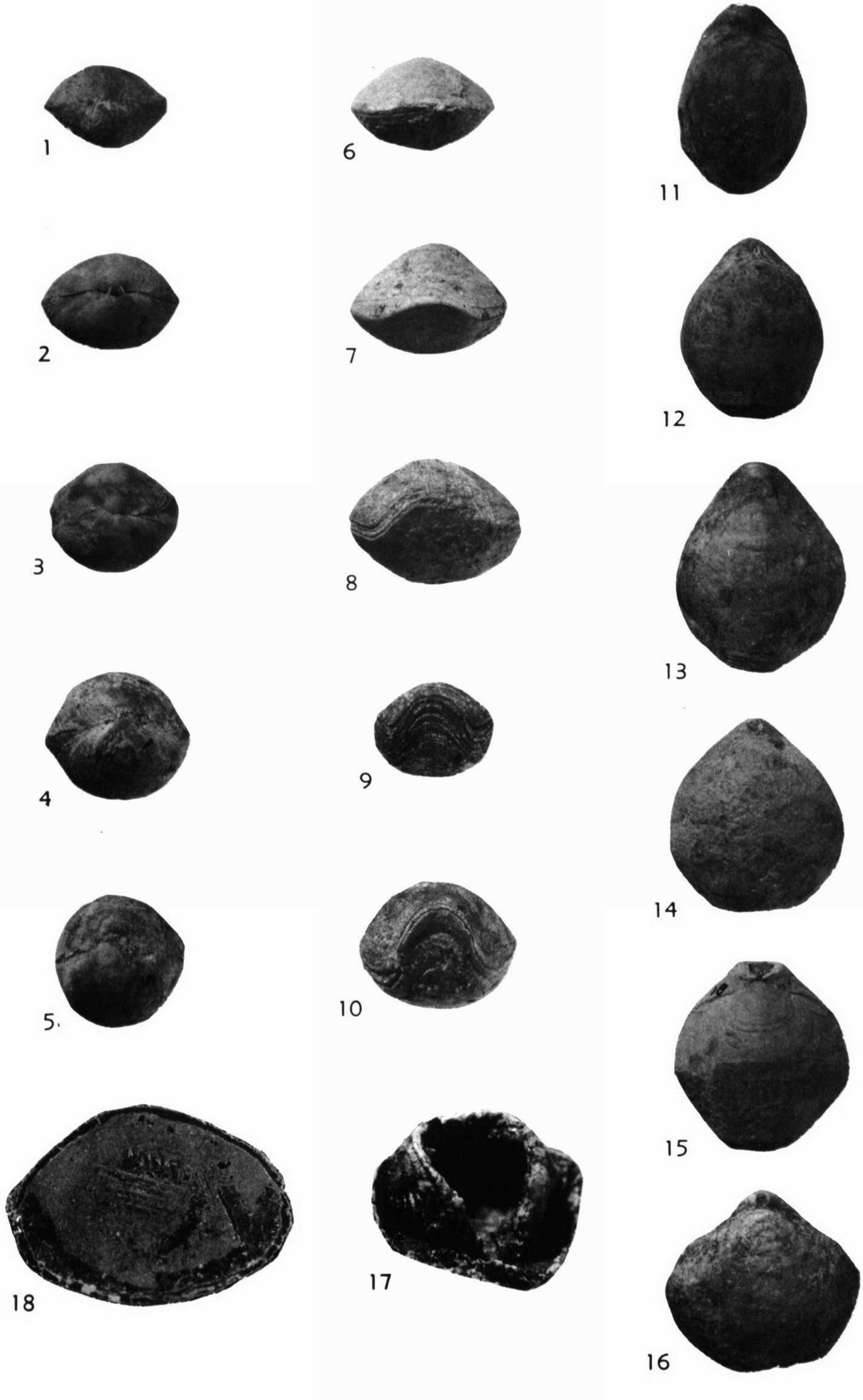
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